Available online at www.sciencedirect.com
ScienceDirect
Biological Control 42 (2007) 9–15
Biological Control
www.elsevier.com/locate/ybcon

Predictions of invasion success of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca vitripennis* (Hemiptera: Cicadellidae), in California using life table statistics and degree–day values

Leigh J. Pilkington *, Mark S. Hoddle

Department of Entomology, University of California, Riverside, CA 92521, USA

Received 1 March 2006; accepted 3 April 2007
Available online 21 April 2007

Abstract

The number of expected generations of *Gonatocerus triguttatus* Girault, a parasitoid of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), in California (USA) was estimated using life table statistics and degree–day requirements. Between 0–18.9 and 0–25.3 generations per year were estimated across different climatic regions in California, using life table and degree–day models, respectively. Temperature-based values for net reproductive rate, R_0, were estimated in California using a laboratory-derived equation and ranged from 0 to approximately 29.4 and analyses indicate that a minimum of 7–7.8 generations (calculated using life table and degree–day models) are required each year to sustain a population of *G. triguttatus* in a given area. Long-term weather data from 381 weather stations across California were used with an Inverse-Distance Weighting algorithm to map various temperature-based demographic estimates for *G. triguttatus* across the entire state of California. This Geographic Information Systems model was used to determine number of *G. triguttatus* generations based on degree–day accumulation, generation time, T_c, and R_o. GIS mapping indicated that the only areas in California that may have climatic conditions favorable for supporting the permanent establishment of invading populations of *G. triguttatus*, should *H. vitripennis* successfully establish year-round populations, are Imperial, San Diego, Riverside, Orange and the southern areas of Santa Barbara, Ventura, Los Angeles and San Bernardino counties. Northern counties in California that experience cooler average year-round temperatures do not appear to be conducive to the establishment of permanent populations of *G. triguttatus*. The mechanisms facilitating *G. triguttatus* invasion and the implications of these temperature-based estimates for biological control of *H. vitripennis* are discussed.
Published by Elsevier Inc.

Keywords: Biological control; Degree–days; Demographics; Generation time; GIS mapping; *Gonatocerus triguttatus*; *Homalodisca vitripennis*; *Homalodisca coagulata*; Invasion; Life table statistics; Net reproductive rate

1. Introduction

Following the successful invasion of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), into California USA (*circa* 1990), French Polynesia (*circa* 1999), Hawaii USA (*circa* 2004), and Easter Island Chile (*circa* 2005), this serious insect pest has demonstrated extremely high rates of population growth and rapid spread (Pilkington et al., 2005). A lack of effective natural enemies in the receiving range, no significant competitors, and climatic conditions favorable for establishment, proliferation, and spread (Hoddle, 2004) in California and other infiltrated areas has contributed, in part, to the high invasion success of *H. vitripennis*. In California, there are many uninfested areas with varying

* Corresponding author. Current address: NSW Department of Primary Industries, Gosford Horticultural Institute, Locked Bag 26 Gosford, NSW, 2250 Australia. Fax: +1 61 2 4348 1910.
E-mail address: leigh.pilkington@dpi.nsw.gov.au (L.J. Pilkington).

1049-9644/$ - see front matter Published by Elsevier Inc.
doi:10.1016/j.biocontrol.2007.04.009

biogeographical attributes that appear to be vulnerable to invasion by *H. vitripennis* as this pest has been observed feeding and reproducing in agricultural, urban, and natural areas that range from the relatively cool California coast to much hotter and arid desert interior regions that are irrigated (Hoddle, 2004).

Gonatocerus triguttatus Girault, (Hymenoptera: Mymaridae) is a solitary endoparasitoid that attacks the eggs of sharpshooters in the cicadellid tribe Proconiini (Triapitsyn et al., 2002). In 2000, *G. triguttatus* was deliberately introduced into California, USA as part of a classical biological control program against *H. vitripennis* (Pilkington et al., 2005). Limited recoveries from some release areas have been made tentatively suggesting *G. triguttatus* may have established localized perennial populations in California (Pilkington et al., 2005). Climate, especially temperature, can have a major influence on the establishment, proliferation, spread, and impact of an organism in a new area (Baker, 2002). To this end, we have studied the reproductive and developmental biology of *G. triguttatus* in the laboratory at constant temperatures to better determine the effects of temperature on basic biological parameters such as development times, degree–day requirements, longevity, fecundity, and sex ratio for this parasitoid (Pilkington and Hoddle, 2007).

The acquisition of thermal units over time above a critical minimum for which development is required (referred to as degree–day accumulation), have been used to predict many aspects of insect life history. The ability to accumulate sufficient degree–days to complete development and begin reproduction in a new area may indicate how vulnerable that region is to invasion by an exotic organism (Sutherst, 2000; Baker, 2002), and whether incursion will be transient due to unfavorable conditions for prolonged periods (Jarvis and Baker, 2001; Hatherly et al., 2005) or potentially permanent due to year-round conditions favorable for growth and reproduction (Sutherst, 2000; Baker, 2002).

Laboratory estimations of degree–day requirements and net reproductive rate, a calculation that is dependent on fecundity and the number of daughters produced per female across a range of experimental temperatures, can be used to determine which temperature ranges are suitable for sustained population growth of a parasitoid (Pilkington and Hoddle, 2007). An understanding of how a temperature range affects estimates of population growth of an invading or deliberately introduced biological control agent can assist with the prediction of invasion success by indicating geographical areas where unfavorable temperature regimens may prevent permanent populations establishing (Hoelmer and Kirk, 2005).

Using laboratory-derived demographic data and long-term climate records it should be possible to assess the establishment and invasion potential of *G. triguttatus* throughout California. This technique has already been used to assess the establishment potential of *G. ashmeadi* Girault (Hymenoptera: Mymaridae) in California in response to continued spread by *H. vitripennis* (Pilkington and Hoddle, 2006b). A better understanding of abiotic factors affecting incursion success by *G. triguttatus* will greatly aid comprehension of potential *H. vitripennis* control, parasitoid spread within invaded ranges, establishment success in new areas where inoculative releases of *G. triguttatus* against *H. vitripennis* are being considered, and intensity of competition and distribution overlap with resident biological control agents. The objectives of the present study were to use developmental and life table statistics to predict the invasion potential of *G. triguttatus* throughout California in response to expected continued range expansion by *H. vitripennis*. To assess invasion potential, laboratory-derived demographic data (Pilkington and Hoddle, 2007) were used to develop models to predict and map using GIS the number of *G. triguttatus* generations and subsequent net reproductive rates for this parasitoid across a range of temperatures (Pilkington and Hoddle, 2006b).

2. Materials and methods

2.1. Collection of California weather data for use in GIS analyses

Daily maximum and minimum temperatures were collected from 121 weather stations maintained by the California Irrigation Management Information System (CIMIS, http://wwwcimis.water.ca.gov) and 260 weather stations maintained by the Western Regional Climate Center (WRCC, http://www.wrcc.dri.edu/). Weather stations for which data were downloaded are all located in California. Daily maximum and minimum temperatures were averaged over 5–10 years of complete weather data between January 1, 1995 and December 31, 2004.

2.2. Calculation of accumulated degree–days for GIS mapping

Degree–day accumulation for *G. triguttatus* was calculated using a Microsoft Excel spreadsheet application (http://biomet.ucdavis.edu, last accessed February 23, 2005) from temperature data downloaded for each of the 381 accessed weather stations. Daily maximum and minimum temperatures, averaged for each weather station, were used to calculate accumulated degree–days for *G. triguttatus* using the single sine method (UC IPM, 2005). The lower developmental threshold value, calculated from the linear portion of the developmental data (Pilkington and Hoddle, 2007), was 10.4 °C and upper lethal threshold used was 38.8 °C.

2.3. Calculation of the number of G. triguttatus generations by location for GIS mapping

Two measures of the number of *G. triguttatus* generations in a given year were calculated for each weather station. The number of generations based on degree–days accumulation above a thermal minimum of 10.4 °C, the point at which the linear portion of the modified Logan model converged on the x-axis, was calculated by dividing each weather station's accumulated degree–days by the number of degree–days, 204, that *G. triguttatus* requires for development (Pilkington and Hoddle, 2007). This returned the number of expected generations at that weather station for the entire year. The second estimation for the yearly number of generations, T_{num}, was calculated by using an adaptation of the fitted model equation for generation time (T_c):

$$T_c = 0.1802\chi^2 - 10.832\chi + 173.99$$

(Pilkington and Hoddle, 2007), where χ is equal to the daily average temperature at each weather station.

The value for T_{num}, the proportion of a generation that was completed at the prevailing average temperature for each weather station, was calculated for each 24 h period by taking the reciprocal of that day's value for generation time calculated from the daily mean temperature at that weather station (Pilkington and Hoddle, 2006b). Temperatures below 10.4 °C were considered too cold and parasitoid development would temporarily cease thereby returning a value of zero at that weather station at that specific time. The formula for calculating the total number of yearly generations, T_{num}, for *G. triguttatus* was:

$$T_{num} = \sum_{\chi \text{ day } 1\ldots365} (1 \div (0.1802\chi^2 - 10.832\chi + 173.99))$$

(derived from Pilkington and Hoddle (2007) Fig. 3, T_c), where χ is equal to the daily average temperature at each weather station.

2.4. Calculation of net reproductive rates (R_o) for GIS mapping

Estimates of the number of generations for each weather station site in California may not reflect an accurate value for generation turnover as this calculation does not take into account the impact of daughters produced by each reproductively competent adult female on the growth of the parasitoid population (Pilkington and Hoddle, 2006b). The demographic statistic for net reproductive rate, R_o, is a robust indication of the capacity for a population to sustain itself or increase in size (Pilkington and Hoddle, 2006a). When the value for R_o is greater than 1.0 the population increases in size. In contrast, when R_o is less than 1.0 then the population is contracting; R_o of one indicates a stable population (Deevey, 1947). The success that an invading population of *G. triguttatus* may experience in a given area was estimated by calculating the average R_o, for each weather station from daily maximum and minimum temperature values. The model estimating R_o across a range of temperatures is (Pilkington and Hoddle, 2007):

$$R_o = -0.5959\chi^2 + 29.2\chi - 302.31$$

where χ is equal to the daily average temperature at each weather station. Daily estimates for R_o were averaged over the entire year to estimate R_o for *G. triguttatus* populations in specific locations. It was assumed that any area where the calculation of the yearly value for R_o resulted in a negative value would preclude the possibility of *G. triguttatus* populations permanently establishing. This result was observed in some areas of California over winter when cold temperatures were predicted to prevent individuals persisting in specific areas because of low reproductive output. Overall means for a geographic point that were returned as negative values were converted to zeroes (representing no establishment potential) and mapped accordingly.

2.5. Construction of GIS maps to assess invasion potential of G. triguttatus in California

The number of generations estimated by degree–day accumulation and generational turnover using the R_o model as calculated for *G. triguttatus* from all weather stations were compiled into a spreadsheet along with the location of the station in decimal degrees of latitude and longitude. The spreadsheet was then imported into ArcGIS 8.3 (ESRI, Redlands, USA). The estimates of number of generations, and of R_o for *G. triguttatus* for each weather station were converted into an ArcGIS shapefile and latitude–longitude coordinates were used to perform a Teale Albers projection.

The ArcGIS Extension Geostatistical Analyst (ESRI, Redlands, USA) was used to generate interpolated grids for estimated values of number of generations using degree–days, and R_o using an Inverse-Distance Weighting (IDW) algorithm that covered the entire state of California. The input parameters for the IDW analysis were:

(1) For each interpolation, 15 weather station sites were used. The default value of 15/10 was used; meaning that in the event that 15 sites are unavailable, the minimum number accepted was 10, a default function that was not required with this dataset as 15 weather stations were always available for analyses.
(2) The spatial shape for including neighboring weather stations was designated to be circular as a directional influence in the data cannot be assumed *a priori* in these analyses.
(3) The default Power Optimization in the Geostatistical Analyst was chosen. The "Power Value" is the distance weight given to a station used in the interpolation. The "Power Value" is inversely weighted so that the contribution of more distant input stations to the interpolation of the data at any given location is less with increasing distance.

3. Results

3.1. GIS mapping of estimated life table statistics

Maps delineating *H. vitripennis* establishment status (total, partial or no establishment) in Californian counties (Fig. 1a), number of generations of *G. triguttatus* calculated by degree–day accumulation (Fig. 1b), number of generations of *G. triguttatus* calculated from the modified life table statistic T_{num} (Fig. 1c), and R_{o} (Fig. 1d) were produced reflecting estimated demographic values across California based on averaged annual temperature data.

Current distribution of *H. vitripennis* in California (Fig. 1a) shows that the initial invasion of the pest is in areas where climatic conditions favor permanent populations. The estimates for the yearly number of generations based on degree–day calculations (Fig. 1b) indicated that *G. triguttatus* would be capable of completing from 0 to 25 generations a year in California. The possible number of generations produced by *G. triguttatus* is severely reduced as populations move north out of the warmer southern counties of Riverside and San Diego and into areas with average temperatures that are cooler. These estimates indicate that in winter months, populations of *G. triguttatus* may continue to reproduce in southern California, but at a much lower rate than observed over summer. Further, this parasitoid may not establish permanent populations or exhibit substantial increases in population size in most of California as average prevailing winter temperatures will be too cool.

In California, the estimated number of generations per year based on the equation for T_{num} indicates that *G. triguttatus* can be expected to range from 0 to approximately 19 generations (Fig. 1c). This produces a smaller range of generation estimates, but is verified by degree–day calculations in that the distribution of generation activity is similar to other estimates. These two estimates of generation numbers, calculated by degree–day accumulation and the equation for T_{num}, do not take into account the number of daughters produced per reproductively active female or the effects of cold temperatures on reproductive output in which populations can maintain themselves thereby preventing a decline that leads to extinction when $R_{\text{o}} < 1.0$.

The value of $R_{\text{o}} = 1$ (i.e., *G. triguttatus* population growth is static) occurs when the average temperature is approximately 14.9 °C (this can be either for one day, week, or an entire year). By substituting this temperature into the equation for T_{num}, a value of approximately seven generations is returned. This suggests that when seven or more generations of *G. triguttatus* are produced yearly, the population will maintain itself or increase, less than seven generations and the population will not be able to persist in an area for an entire year. Much of California north of Ventura County exhibits temperatures that are on the threshold of this critical generation number and populations in this southern-central area of California, according to R_{o} estimates, may be stable year round at best, but in an environment unsuitable for rapid and sustained population growth. In these areas of California, unfavorable cold weather events could easily extirpate tenuous populations of *G. triguttatus*.

The values returned for R_{o} (Fig. 1d) range from 0 to approximately 26 and indicate that many of the counties in California may be unsuitable for *G. triguttatus* due to low winter temperatures. The basic shape of the darker blue colors shown in Fig. 1d broadly mirrors the shape seen in both of the generation estimate maps and indicates that the central eastern counties of California may be unsuitable for permanent establishment of *G. triguttatus* populations and the extreme southern regions of California may be the only areas suitable for perennial establishment of this exotic parasitoid.

4. Discussion

Climate, especially inclement weather conditions, can significantly affect the ability of an insect population to invade and establish in an area outside its native range (Crawley, 1987). The length of time the population is subjected to deleterious temperatures (too low or high) affects the population's ability to recover from adverse climate effects and continue development (Jarvis and Baker, 2001). Modeling of demographic statistics as influenced by temperature from long-term weather data records for the receiving area may provide an indication of the potential success or failure for an invading insect species to establish itself permanently in a new area, and for the population growth of that incipient population.

Results of this study have estimated the potential invasion success by *G. triguttatus* into uncolonized areas of California. The results of these temperature-based analyses indicate where *G. triguttatus* could be expected to spread based on climatic conditions only. Seasonal host availability has not been considered but will obviously have a major impact on the spread of this parasitoid in California. Consequently, these estimations need to be viewed cautiously and used as a comparative tool between regions rather than a definitive number of expected parasitoid generational turnover in any area. A major short-coming with managing *H. vitripennis* in California (and elsewhere) and accurately predicting its invasion potential is the severe paucity of demographic data for this pest and the influence of temperature on its development and longevity. The availability of such data would enable comparisons between *H. vitripennis* and its natural enemies and would better enable predictions of parasitoid spread in relation to the target pest.

The number of degree–days required to move from one generation to the next is a valuable tool in estimating the establishment success of an insect (Tullett et al., 2004) and the calculation of the number of generations from this estimation is an accurate estimate of the potential success of an invading organism in a given area (Hart et al., 2002). Developmental data experimentally derived under varying temperatures will allow for diagnostic mapping

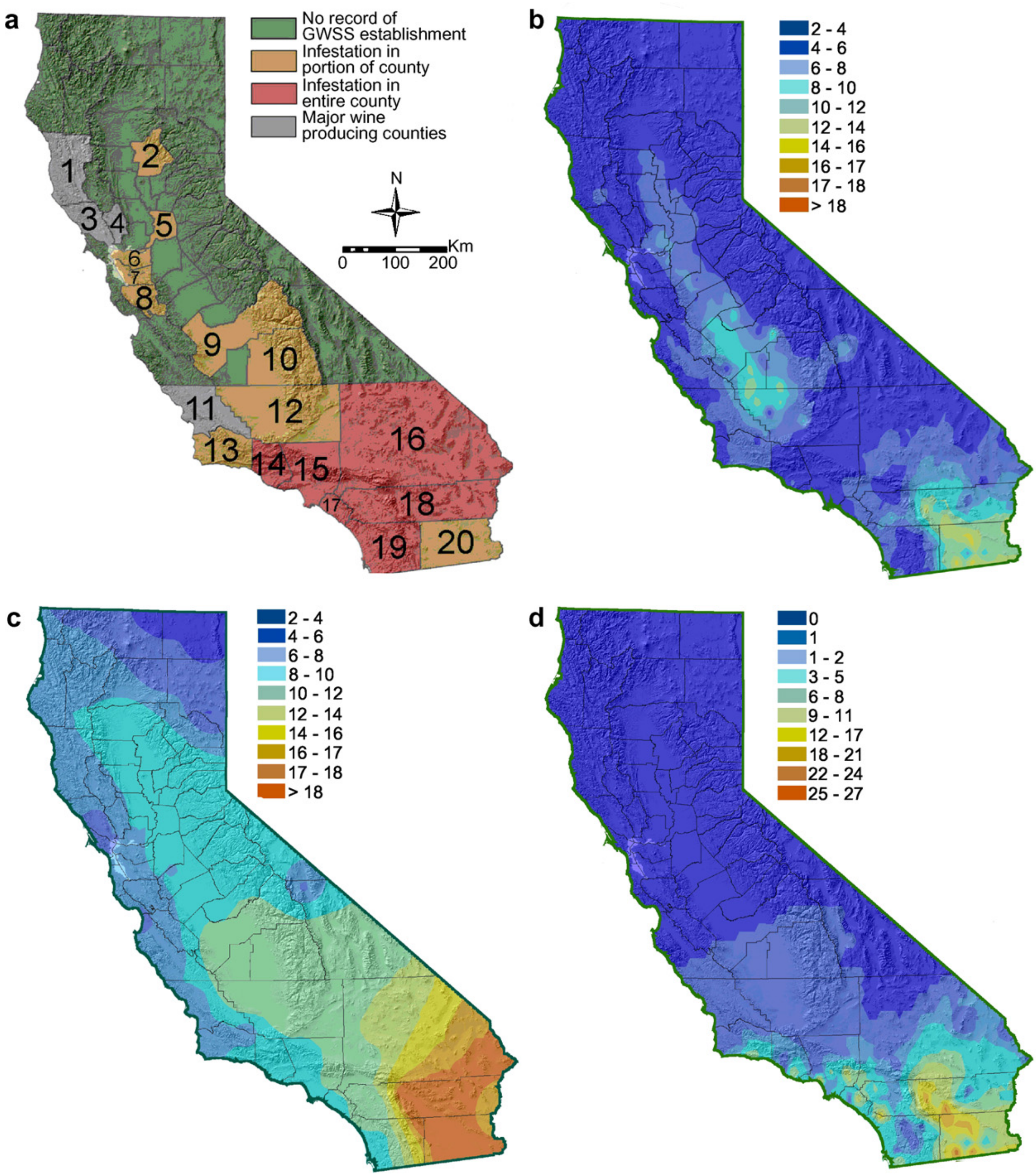

Fig. 1. Geographical information systems mapping of estimated life table statistics for the parasitoid *Gonatocerus triguttatus* in California, USA; (a) Counties in California and the status of *Homalodisca vitripennis* populations in each area 1. Mendocino 2. Butte 3. Sonoma 4. Napa 5. Sacramento 6. Contra Costa 7. Alameda 8. Santa Clara 9. Fresno 10. Tulare 11. San Luis Obispo 12. Kern 13. Santa Barbara 14. Ventura 15. Los Angeles 16. San Bernardino 17. Orange 18. Riverside 19. San Diego 20. Imperial; (b) estimated number of generations populations of *G. triguttatus* may experience in each area calculated by dividing the year's accumulated degree–days by the total degree–days required by *G. triguttatus* for development; (c) estimated number of generations that hypothetical populations of *G. triguttatus* may experience in each area calculated by applying historical weather data to the formula for yearly generations, T_{num}, derived from the life table statistic for generation time, T_c and; (d) estimation of the yearly value for net reproductive rate, R_o, derived by applying historical weather data to the formula for R_o. For (b)–(d) the colored legend indicates the value of the particular statistic of interest for an entire year.

of areas based on degree–day requirements when estimates of reproductive output across a range of temperatures are not available.

Results presented here using R_o estimates indicate that counties in southern California (i.e., all those to south of Ventura County) have, host availability notwithstanding, year-round climatic conditions favorable for *G. triguttatus* and this correlates well with the current known distribution of *G. triguttatus* in California. *G. triguttatus* has been released as part of the California Department of Food and Agriculture's release program in the California counties of Los Angeles, Kern, Ventura, Santa Clara, Orange, Riverside, San Bernardino, and San Diego (Anon, 2002). The parasitoid has only been recovered from the counties of Riverside, Ventura, Orange, and San Diego in California (Anon, 2002). All these counties from which *G. triguttatus* recoveries have been made fall within areas of California where *G. triguttatus* is predicted to have high potential for reproductive and development success based on laboratory-derived estimates of its climatic requirements. Notably, the parasitoid has not been recovered from more northerly, colder counties such as Kern and Santa Clara, possibly due to the inability of the released populations to overcome the colder winter temperatures. This result is suggestive that GIS modeling of developmental and demographic attributes may be accurate indicating that *G. triguttatus* is an unsuitable biological control agent for *H. vitripennis* in much of California and its invasion potential out of areas where it has established is very low.

All counties that have a R_o value <1.0 occur in central and northern California, above Ventura County. These areas are probably incapable of supporting invading populations of *G. triguttatus* that result in perennial populations. Winter temperatures in these northern areas appear to be deleterious to parasitoid populations and *G. triguttatus* would be expected to have trouble recovering to fully infiltrate these areas each year regardless of host availability. The effect of temperatures experienced in these areas on *H. vitripennis* are unknown, but inferential modeling suggests areas in the extreme north of California and southern Oregon will be too cold for this pest to persist (Hoddle, 2004). Consequently, it would appear that much of central California, where *H. vitripennis* is known to be present, will be unsuitable for *G. triguttatus* and climate will prevent permanent parasitoid populations establishing. Of particular concern are the counties highlighted as important wine growing regions in California as these northern wine growing districts appear to have environmental conditions that are inhospitable for year-round persistence of *G. triguttatus* as well as *G. ashmeadi* (Pilkington and Hoddle, 2006b), the dominant biological control agent of *H. vitripennis* in California at present. Equivalent information on the influence of temperature on the developmental and reproductive biology of *H. vitripennis* is lacking and studies are urgently needed to address this important knowledge gap so deductive estimates of invasion by this pest into California's premier wine growing areas can be made. Inductive modeling suggests northern California wine growing regions may be vulnerable to invasion by *H. vitripennis* (Hoddle, 2004).

Approximate degree–day estimates for *H. vitripennis* have been determined to be 530 degree–days to complete development from egg to adult (Pilkington and Hoddle, 2006a). In contrast, *G. triguttatus* requires 204 degree–days for development from oviposition to emergence of adult stages (Pilkington and Hoddle, 2007). This parasitoid could potentially experience generational turnover of more than double that of *H. vitripennis*, but suffer severely reduced biological control efficacy in much of California where *H. vitripennis* is present due to its intolerance of low temperatures. Relative rates of generational turnover suggest that when the local climate allows *G. triguttatus* to successfully establish a population and maintain that population perennially, it could potentially be an extremely efficient control agent of *H. vitripennis* populations. This may be evidenced by the low numbers of *H. vitripennis* populations in the home range of southeastern USA and northeastern Mexico where *G. triguttatus* dominates the parasitoid guild (Pilkington et al., 2005).

In conclusion, the results of this work indicate that a potential limiting factor affecting invasion success in California by *G. triguttatus* may be the climate in the receiving area. Where climatic conditions are favorable and *H. vitripennis* is present, high generational turnover by the parasitoid would be anticipated to provide significant suppression of the target pest if interspecific competition for host eggs is not a limiting factor. Areas in which *H. vitripennis* can invade and establish viable year-round populations but in which temperatures are not suitable for year-round persistence of *G. triguttatus* may allow this pest to escape from attack by this natural enemy. If warranted and cost effective, *G. triguttatus* may be a candidate for seasonal inoculative releases during the warmer months of summer in Californian counties north of Ventura and San Bernardino, as it appears that this parasitoid will be incapable of establishing perennial, year-round populations in these areas for *H. vitripennis* control. This work has shown that an understanding of the relationship between reproductive biology and temperature is crucial to predicting invasion success of natural enemies and interpreting and understanding the outcomes of biological control programs in relation to climatic influences.

Acknowledgments

This work was supported in part by funds awarded by the California Department of Food and Agriculture's Pierce's Disease Control Program. Kris Lynn-Patterson, University of California Kearney Agricultural Center, is acknowledged for her assistance with GIS output.

References

Anon, 2002. Biological control of the glassy-winged sharpshooter: Monthly report, August 2002 [Online]. Available at: <http://www.cdfa.ca.gov/phpps/pdcp/BioCtrlRep/Doc/gwBioRep082002.PDF/> (verified 10 June 2005).

Baker, R.H.A., 2002. Predicting the limits to the potential distribution of alien crop pests. In: Hallman, G.J., Schwalbe, C.P. (Eds.), Invasive Arthropods in Agriculture. Problems and Solutions. Science Publishers, Inc., Enfield, USA, pp. 207–241.

Crawley, M.J., 1987. What makes a community invasible? Colonization, Succession and Stability; The 26th Symposium of The British Ecological Society Symposium Held Jointly with the Linnean Society of London, 26, 429–454.

Deevey Jr., E.S., 1947. Life tables for natural populations of animals. Q. Rev. Biol. 22, 283–314.

Hart, A.J., Tullett, A.G., Bale, J.S., Walters, K.F.A., 2002. Effects of temperature on the establishment potential in the UK of the non-native glasshouse biocontrol agent *Macrolophus caliginosus*. Physiol. Entomol. 27, 112–123.

Hatherly, I.S., Hart, A.J., Tullett, A.G., Bale, J.S., 2005. Use of thermal data as a screen for the establishment potential of non-native biological control agents in the UK. BioControl 50, 687–698.

Hoddle, M.S., 2004. The potential adventive geographic range of glassy-winged sharpshooter, *Homalodisca coagulata* and the grape pathogen *Xylella fastidiosa*: implications for California and other grape growing regions of the world. Crop Prot. 23, 691–699.

Hoelmer, K.A., Kirk, A.A., 2005. Selecting arthropod biological control agents against arthropod pests: can the science be improved to decrease the risk of releasing ineffective agents? Biol. Control 34, 255–264.

Jarvis, C.H., Baker, R.H.A., 2001. Risk assessment for nonindigenous pests: I. Mapping the outputs of phenology models to assess the likelihood of establishment. Divers. Distrib. 7, 223–235.

Pilkington, L.J., Hoddle, M.S., 2006a. Reproductive and developmental biology of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae). Biol. Control. 37, 266–275.

Pilkington, L.J., Hoddle, M.S., 2006b. Use of life table statistics and degree–day values to predict the invasion success of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae), in California. Biol. Control. 37, 276–283.

Pilkington, L.J., Hoddle, M.S., 2007. Use of life tables to quantify reproductive and developmental biology of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca vitripennis* (Hemiptera: Cicadellidae). Biol. Control. doi:10.1016/j.biocontrol.2007.04.006.

Pilkington, L.J., Irvin, N.A., Boyd, E.A., Hoddle, M.S., Triapitsyn, S.V., Carey, B.G., Jones, W.A., Morgan, D.J.W., 2005. Introduced parasitic wasps could control glassy-winged sharpshooter. Calif. Agric. 59 (4), 223–228.

Sutherst, R.W., 2000. Change and invasive species: A conceptual framework. In: Mooney, H.A., Hobbs, R.J. (Eds.), Invasive Species in a Changing World. Island Press, Washington, DC, pp. 211–240.

Triapitsyn, S.V., Hoddle, M.S., Morgan, D.J.W., 2002. A new distribution and host record for *Gonatocerus triguttatus* in Florida, with notes on *Acmopolynema sema* (Hymenoptera: Mymaridae). Fla. Entomol. 85, 654–655.

Tullett, A.G., Hart, A.J., Worland, M.R., Bale, J.S., 2004. Assessing the effects of low temperature on the establishment potential in Britain of the non-native biological control agent *Eretmocerus eremicus*. Physiol. Entomol. 29, 363–371.

UC IPM, 2005. UC IPM Online. Statewide Integrated Pest Management Progam—How To Manage Pests: Degree Days. [Online]. Available at: <http://axp.ipm.ucdavis.edu/WEATHER/ddconcepts.html/> (verified 20 December, 2005).